Microclimate: an Alternative to Tree Vigor as a Basis for Mountain Pine Beetle Infestations

Dale L. Bartos
Gene D. Amman
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INTRODUCTION

Temperature is an important factor in the ecology of insects. It affects the physical conditions of habitats and the insects themselves (Kelling 1960). In the case of the mountain pine beetle (MPB) (Dendroctonus ponderosae Hopkins [Coleoptera: Curculionidae]), observations were made on the effects of extremely high (Patterson 1930) and low temperatures (Somme 1964; Yuill 1941). Between the extremes is an optimum zone of temperature that may be modified by other climatic factors (Radinsky 1962).

Thinning forests causes subtle changes not only in tree physiology (Nobker and Hodges 1988) but also in incident radiation, temperature, light (Befenzyer and Lull 1985), and wind speed. These changes brought about by thinning lodgepole pine (LPP) (Pinus contorta var. latifolia Engelm.) forests have profound effects on MPB activity (Schmitt and others, in press) resulting in reduced tree mortality in thinned stands (McGregor and others 1987). The avculrative practices of thinning have been used in the past as a way of increasing tree vigor (Graham and Knight 1986; Keene 1958), which in turn could make the residual trees better able to resist attacks by MPB. The removal of large-diameter lodgepole pine, which are preferred by MPB, can also result in reductions in tree loss during epidemics (McGregor and others 1987). Reduced infestation by MPB occurs immediately following partial cutting of LPP stands (McGregor and others 1987) and before residual trees could express resistance due to increases in growth and vigor as measured by periodic growth rates and growth efficiency (Amman and others 1988). This phenomenon suggests that factors other than vigor may be responsible for reduced MPB infestation.

Subtle changes in chemistry of residual trees following thinning of stands is one possibility. Biochemical responses detected by the beetles could cause them to avoid trees in thinnings. Nobker and Hodges (1988) studied the effects of thinning and thinning-related injury to loblolly pine (P. taeda L.) by measuring oxygen and carbon dioxide exchange rates, water flow rate, total flow, and relative viscosity of visual temperature. They found total flow and relative viscosity were significantly different by month and treatment, with the greatest increase in trees receiving only basal wounding. Maxwell and others (1987), also studied effects of thinning loblolly pine, found resin flow rates, starch concentration in phloem tissue, relative growth, and bark and phloem thickness were greater in trees in thinned plots than trees in control or fertilized plots, 6 years after treatments were applied. Raffa and Berryman (1980) studied physiological differences between lodgepole pine resistant and susceptible to MPB and associated microorganisms. They found no relationship between resistance and daily rate of resin flow, rate of resin crystallization, monomeric content, monomer composition, or current growth rate. Resistant trees responded to artificial inoculation of fungi re ridicated by MPB by forming greater quantities of resin than susceptible trees. However, Petersen (1977), in a field test of the fungal inoculation method of distinguishing resistant and nonresistant trees, found the method ineffective. Therefore, we chose to explore the microclimate of the altered stand because (1) microclimate changes immediately following tree removal from the stand and (2) residual trees in the stands were slow to increase growth. The objective of this paper is to present microclimatic differences we observed between thinned and unthinned LPP stands and discuss beetle behavior in response to these differences.

METHODS AND MATERIALS

The study site is south of Mountain View, WY, on the north slope of the Uinta Mountains in northeastern Utah, at an elevation of 2,985 m. A thinned and an adjacent unthinned stand of LPP, both of which had current beetle infestation, were selected for study of microclimatic difference. An additional thinned and an adjacent unthinned stand of LPP, both of which had beetles in infestation, were selected for study of beetle response to phemene-baited traps.

Stand Characteristics

Characteristics of the thinned and unthinned LPP stands studied are differences were determined through variable plot 10 (10 BAPF) cruising. Plots were 50 m apart in a grid pattern in each stand. Trees on the plot were tallied as alive or dead by cause of death and were measured for diameter at breast height (dbh). The dominant or codominant tree closest to plot center was
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INTRODUCTION

Temperature is an important factor in the ecology of insects. It affects the physical conditions of habitats and the insects themselves (Wells 1960). In the case of mountain pine beetle (MPB) (Dendroctonus ponderosae Hopkins [Coleoptera: Scolytidae]), observations were made on the effects of extremely high (Patterson 1930) and low temperatures (Somme 1964; Yulii 1943). Between the extremes is an optimum zone of temperature that may be modified by other microclimatic factors (Radinsky 1969).

Thinning forests causes subtle changes not only in tree physiology (Nohrke and Hodges 1984) but also in incident radiation, temperature, light (Brenner and Lull 1965), and wind. These changes brought about by thinning lodgepole pine (LPP) [Pinus contorta var. latifolia Engelm.] forests have profound effects on MPB activity (Schmitt and others, in press) resulting in reduced tree mortality in thinned stands (McGregor and others 1987).

The climatological practice of thinning has been used in the past as a way of increasing tree vigor (Graham and Knight 1965; Reed 1968), which in turn could make the residual trees better able to resist attacks by MPB. The removal of large-diameter lodgepole pine, which are preferred by MPB, can also result in reductions in tree loss during epidemics (McGregor and others 1987). Reduced infestation by MPB occurs immediately following partial cutting of LPP stands (McGregor and others 1987) and before residual trees could express resistance due to increases in growth and vigor as measured by periodic growth rates and growth efficiency (Amman and others 1988). This phenomenon suggests that factors other than vigor may be responsible for reduced MPB infestation.

Changes in chemistry of residual trees following thinning of stands is one possibility. Biochemical responses detected by the beetles could cause them to avoid trees in thinnings. Nohrke and Hodges (1983) studied the effects of thinning and thinning-related injury to lodgepole pine (P. contorta L.) by measuring chlorophyll exudation pressure, electrical resistance, resin flow rate, total flow, and relative viscosity of resin. They found total flow and relative viscosity were significantly different by month and treatment, with the greatest increase in trees receiving only basal wounding. Matson and others (1987), also studying effects of thinning lodgepole pine, found resin flow rates, starch concentration in phloem tissues, relative growth, and bark and phloem thickness were greater in trees in thinned plots than those in control or fertilized plots, 6 years after treatments were applied. Raffa and Barryman (1986) studied physiological differences between lodgepole pine resistant and susceptible to MPB and associated microorganisms. They found no relationship between resistance and daily rate of resin flow, rate of resin crystallization, monoterpane content, monoterpane composition, or current growth rate. Resistant trees responded to artificial inoculation of fungi by resinating MPB by forming greater quantities of resin than susceptible trees. However, Peterson (1977), in a field test of the fungal inoculation method of distinguishing resistant and nonresistant trees, found the method ineffective. Therefore, we chose to explore the microclimate of the thinned stand because (1) microclimate changes immediately following tree removal from the stand and (2) residual trees in the stand were slow to increase growth. The objective of this paper is to present microclimatic differences we observed between thinned and unthinned LPP stands and to discuss beetle behavior in response to these differences.

METHODS AND MATERIALS

The study site is south of Mountain View, WY, on the north slope of the Uinta Mountains in northeastern Utah, at an elevation of 2,665 m. A thinned and an adjacent unthinned stand of LPP, both of which had current beetle infestation, were selected for study of microclimatic differences. An additional thinned and an adjacent unthinned stand of LPP, both of which had no history of beetle infestation, were selected for study of beetle response to phytotoxic halved traps.

Stand Characteristics

Characteristics of the thinned and unthinned LPP stands studied in this project were determined through variable plot (10 BAP) cruising. Plots were 50 m apart in a grid pattern in each stand. Trees on the plot were tallied as live or dead by cause of death and were measured for diameter at breast height (d.b.h.). The dominant or codominant tree closest to plot center was
Temperature—Thermoelectric pyrometers were connected to the micrologger to measure temperature at the following sites on the sample trees:

1. At breast height, 1.4 m above ground, on the bark surface and immediately below the surface for both the north and south sides of the tree. This measure was positioned to measure temperature of the tree's phloem. Phloem is the substrata in which MBP adults are found and lay eggs and also serves as the food source of developing larvae.

2. In the lower third of the crown on the bark surface, on both the north and south sides of the tree (about 3 m above ground) where the micrologger was situated. This sample area was to represent air temperature of the inter-space of the stand.

Incident Solar Radiation—LI-COR quantum sensors were used to measure incident solar radiation. These sensors measure photosynthetically active radiation in the 400- to 700-nm waveband. Values reported were for the average energy flux density for the sampled period and are given in units of 1,000 μmol m⁻² s⁻¹. For both treatments, these solar sensors were placed on one location: one on the tree, one at breast height on each sample tree, and one in the lower third of the crown. Solar sensors attached to the tree were placed on the north side.

Windspeed—Windspeed sensors were standard 3-cup anemometers, which were connected to the micrologger. Data were reported in units of kilometers per hour. Two sensors were placed on either side of the thinned and unthinned stands. One sensor was placed on the tower (about 3 m above ground), the other in the lower third of the crown of the sample tree.

Wind Direction—The light-weight wind direction sensor we used was an air-flow vane and a potentiometer, which produced an output that varied proportionally to the wind direction. Output was recorded in degrees and varied between 0° and 360°. A sensor was placed on the tower, which would allow minimum interference from the trees in each of the stands.

Stand Temperatures—Temperatures in the thinned and unthinned stands were monitored with microclimate measurements, which were obtained to a random sample of temperature between 10 a.m. and 2 p.m. on August 4, 1986. This period was selected to record maximum solar penetration into the stand. The survey was conducted on 10 transect lines 20 m apart; observations were made at 30-m intervals along each transect line. Temperatures of the ground and the north and south sides of the living tree nearest to plot center were obtained with an infrared thermometer (Wahl Digital Heat Spy Model DH14-14). Tree temperatures were taken at breast height. Each survey line passed through both thinned and unthinned stands and was large enough to have occurred if one stand had been completely surveyed before starting the survey of the other stand.

Beetle Response

Beetle response to thinned and unthinned stands was determined by placing 20 pheromone-baited traps in the general vicinity of the microclimate study. Three green funnel traps were hung in a thinned stand and three in an adjacent unthinned stand. Traps were left in place within stands and 300 m apart between stands. These stands were approximately 1 km north of the stands where microclimate observations were made. There were no beetle-infested trees in the two stands at the time of trapping. The traps were baited with the standard MBP lure (Vito Tech, Inc.), consisting of 1:1:2 mixtures of luteolene, epulivarin, and myrcene. Beetles were collected from the traps weekly for 4 weeks, starting on June 15 to September 3, 1986, the summer before microclimate observations were made. Beetles were taken to a laboratory where they were sexed and counted.

Data Analysis

Characteristics and temperatures of thinned and unthinned stands obtained during stand surveys were subjected to analysis of variance to test for significant differences. Statistical analysis of data from the micrologger was not possible because we had enough equipment to monitor microclimate of one tree in each of the two stands. Therefore, we used a time series analysis system software package for microcomputers to manipulate various combinations of factors to show trends that exist between the thinned and unthinned stands, as well as within the thinned and unthinned stands. A smoothing technique was used to reduce some of the inherent variation. We accomplished this smoothing by calculating a moving average of the raw data. These smoothed curves were better able to show consistent trends between similar factors than had previously been observed. Because the version of the program used would accept only 50 values, we used the hour averages to look at the overall trends for the 33 days. The moving average was deleted from the plot and the next hour time period (49 hours versus 5 hours) was used to obtain the smoothed average. Next, to see if we were making a detail, we used the 15-minute average, which plotted the 5 days that encompassed the peak flight period (July day 210). Finally, we plotted averaged smoothed data for the day that peak flight occurred (midnight to midnight).

RESULTS

We looked at the results in terms of stand characteristics, microclimate, and beetle response.

Stand Characteristics

Characteristics of the thinned stand in which microclimate was taken were determined on an average basal area of 22.1 m², b/a, a density of 707.8 stems/ha, a mean average large tree (approximately 20 minutes used per line) that would have occurred if one stand had been completely surveyed before starting the survey of the other stand.

Beetle Response

Beetle response to thinned and unthinned stands was determined by placing 20 pheromone-baited traps in the general vicinity of the microclimate study. Three green funnel traps were hung in a thinned stand and three in an adjacent unthinned stand. Traps were left in place within stands and 300 m apart between stands. These stands were approximately 1 km north of the stands where microclimate observations were made. There were no beetle-infested trees in the two stands at the time of trapping. The traps were baited with the standard MBP lure (Vito Tech, Inc.), consisting of 1:1:2 mixtures of luteolene, epulivarin, and myrcene. Beetles were collected from the traps weekly for 4 weeks, starting on June 15 to September 3, 1986, the summer before microclimate observations were made. Beetles were taken to a laboratory where they were sexed and counted.

Stand Microclimate

Temperature (23 Days)—Curves for a 23-day period obtained via smoothing raw data appeared similar between the north and south sides of the sampled tree at breast height in the thinned stand. The average temperature varied between 9 °C at the beginning of the 23 days to a high of approximately 18 °C around August 5, 1986. Both sets of curves show close correlation between the surface and phloem temperatures. However, a slight separation (0.5 °C) was noticed for the south side of the tree.

Similar traces were observed between the thinned and unthinned stand. Subsurface temperatures reflect what occurs on the bark surface but with slightly less magnitude. The phloem curve for the south side in the thinned stand was consistently 1 to 2 °C higher than the phloem curve in the unthinned stand (fig. 2A), while the surface temperatures on the south side in the thinned stand (fig. 2B) responded with a 1 to 3 °C greater difference than that in the unthinned stand.

Less difference was observed between the thinned and unthinned stands when comparisons were made on the north side of the sampled trees. Traces of the curves on the north side were similar to those on the south side. However, as expected, the south side was consistently 3 to 4 °C higher. On the north side, curves for the phloem temperature mimicked the surface temperature, and a difference of less than 0.5 °C between the thinned and unthinned stand was observed.

Temperature (5 Days)—Smoothing over a 5-day period was done to express more detail for any one 24-hour period. This information was partially masked when smoothing was done for the full 23 days. Initially, we looked at pairs of curves showing within-24-hour differences at breast height in both treatments. Similar responses were observed, and figure 5 shows the various combinations. Over a 24-hour period, there is a reversal in dominance of the two temperature curves. From early afternoon through late evening, surface temperature is warmer than phloem temperature, but for the rest of the period it is just the opposite. These trends are consistent from day to day over the 5 days. At the point of maximum separation, there is 0-5 °C difference. We see much more separation in the averaged temperature curves (fig. 4) when we make comparisons between the same sample points for the two treatments. This information is an elaboration of the previous results (fig. 2). The thinned stand always had the higher temperature. The difference ranged from 2 to 3.5 °C, and the highest difference occurred during the hottest part of the day.
Temperature—Thermocouple psychrometers were connected to the micrologger to measure temperature at the following points on the sample trees:

1. At breast height, 1.4 m above ground, on the bark surface and immediately below the surface for both the north and south sides of the tree. The horizontal surface probe was positioned to measure temperature of the tree phloem. Phloem is the substrate in which MPB adults lay eggs and also serves as the food source of developing larvae.

2. In the lower third of the crown on the bark surface, both on the north and south sides of the tree.

3. On the lowermost branch (about 2.0 m above ground) where the micrologger was situated. This sample area was to represent air temperature of the inter-space of the stand.

Incident Solar Radiation—LI-COR quantum sensors were used to measure incident solar radiation. These sensors measure photosynthetically active radiation in the 400–700 nm wavelength. Values reported were for the average energy flux density for the sampled period and were given in units of 1,000 μmol/m2/s. For both treatments, these solar sensors were placed at the locations one on the tower, one at breast height on each sample tree, and one in the lower third of the crown. Solar sensors attached to the tree were placed on the north side.

Wind Speed—Wind speed sensors were standard 3-cup anemometers, which were connected to the micrologger. Data were reported in units of kilometers per hour. Two sensors were placed on the tower (above the thinned and unthinned stands). One sensor was placed on the tower (about 3 m above ground), the other in the lower third of the crown. Solar sensors attached to the tree were placed on the north side.

Windspeed—Wind speed sensors were standard 3-cup anemometers, which were connected to the micrologger. Data were reported in units of kilometers per hour. Two sensors were placed on the tower (above the thinned and unthinned stands). One sensor was placed on the tower (about 3 m above ground), the other in the lower third of the crown. Solar sensors attached to the tree were placed on the north side.

Rainfall—Recorded using tipping-bucket rain gauges. Values reported were for the average rainfall for the sampled period and were given in units of millimeters. For both treatments, these rainfall sensors were placed at the locations one on the tower, one at breast height on each sample tree, and one in the lower third of the crown. Solar sensors attached to the tree were placed on the north side.

Stand Temperature—Temperatures in the thinned and unthinned stands subjected to microclimate measurement were surveyed to obtain a random sample of temperatures between 10:00 and 13:30, the observations were made at 20-min intervals above the living tree neared to plot center were obtained using a thermistor (Wahl Digital Rain Syst Model DHR-14). Temperatures were taken at breast height. Each survey line passed through both thinned and unthinned stands and was long enough to include large time lag (approximately 20 minutes used per line) that would have occurred if one stand had been completely surveyed before starting the survey of the other stand.

Beetle Response

Beetle response to thinned and unthinned stands was determined by setting up pheromone-treated traps in the general vicinities of the microclimate study. Three Lindgren funnel traps were hung in a thinned stand and three in an adjacent unthinned stand. Traps were 100 m apart within stands and 300 m apart between stands. The stands were approximately 1 km north of the stands where microclimate observations were made. No beemel-infested trees in the two stands at the time of trapping. The traps were baited with the standard MPB lure (Pheromone Technology Co. Lincoln, Neb.; ecosan, trichlorfon, and myrcene). Beetles were collected from the traps weekly for four weeks or until 15 September 1985, the summer before microclimate observation were made. Beetles were taken to a laboratory where they were sexed and counted.

Data Analysis

Characteristics and temperatures of thinned and unthinned stands observed during stand surveys were subjected to analysis of variance to test for significant differences. Statistical analysis of data from the microclimater was not possible because we had only enough equipment to monitor microclimate of one tree in each of the two stands. Therefore, we used a time series analysis system software package for microclimate to manipulate various combinations of factors to show trends that exist between the thinned and unthinned stands, as well as within the thinned and unthinned stands plotted, and a smoothing technique was used to reduce some of the inherent variation. We accomplished this smoothing by calculating a moving average of the raw data. These smoothed curve was better able to show consistent trends between similar factors than had previously been observed. Because the version of the program used would accept only 500 values, we used the hour averages to look at the overall trends for the data. More variance was deleted because the data were plotted, and the 5 days that encompassed the peak flight period (Julian day 210). Finally, we plotted averaged smoothed data for the day that peak flight occurred (midnight to midnight).

RESULTS

We looked at the results in terms of stand characteristics, microclimate, and beetle response.

Stand Characteristics

Characteristics of the thinned stand in which microclimate was monitored included an average basal area of 22.1 m2/ha, a density of 707.8 stems/ha, and an average diameter of 20.2 cm. Dominant and codominant trees averaged 15.1 m in height, with live crown 52 percent of total height. In contrast, the adjacent unthinned stand had a basal area of 37.0 m2/ha, a density of 1,095 trees/ha, and an average diameter of 18.6 cm. Dominant and codominant trees averaged 15.1 m in height, with live crown 53 percent of total height (Table 1). Of these stand characteristics, only the stand density measures (basal area and trees per hectare) were significantly different between stands (P = 0.01).

Stand Microclimate

Temperature (24 Days)—Curves for a 24-day period obtained via sensing raw data appeared similar between the north and south sides of the sample trees at breast height in the thinned stand. The average temperature varied between 9 °C at the beginning of the 23 days to a high of approximately 18 °C around August 5, 1986. Both sets of curves show close correlation between the surface and phloem temperatures. However, a slight separation (0.5 °C) was noticed for the south side of the tree.

Similar traces were observed between the thinned and unthinned stand. Subsurface temperatures reflect what occurs on the bark surface but with slightly less magnitude. The phloem curve for the south side in the thinned stand was consistently 1 to 2 °C higher than the phloem curve in the unthinned stand (Fig. 2A), while the surface temperature on the south side in the thinned stand (Fig. 2B) responded with a 1 to 2 °C greater difference than that in the unthinned stand.

Less difference was observed between the thinned and unthinned stands when comparisons were made on the north side of the sampled trees. Trends of the curves on the north side were similar to those on the south side. However, as expected, the south side was consistently 3 to 4 °C higher. On the north side, curves for the phloem temperature mimicked the surface temperature, and a difference of less than 0.5 °C between the thinned and unthinned stand was observed.

Temperature (5 Days)—Smoothing over a 5-day period and comparing as detailed for any one 24-hour period. This information was partially masked when smoothing was done for the full 23 days. Initially, we looked at pairs of curves showing within-tree differences at breast height in both treatments. Similar responses were observed, and Figure 3 shows the various combinations. Over a 24-hour period, there is a reversal in dominance of the two temperature curves. From early afternoon through late evening, surface temperature is warmer than phloem temperature, but for the rest of the period it is just the opposite. These trends are consistent from day to day over the 5 days. At the point of maximum separation, there is a 0.5 °C difference. We see much more separation in the averaged temperature curves (Fig. 4) when we make comparisons between the same sample points for the two treatments. This information is an elaboration of the previous results (Fig. 3). The thinned stand always had the higher temperature. The difference ranged from 2 to 5.5 °C, and the biggest difference occurred during the hottest part of the day.
Table 1—Some average characteristics of the thinned and unthinned stands monitored for microclimatic differences (includes trees 12.7 cm and larger d.b.h.) in northern Utah.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Lododpole pine per hectare</th>
<th>Killed by MPR</th>
<th>Basal area</th>
<th>Diameter at breast height</th>
<th>Dominant/ codominant height</th>
<th>Crown length percentage of total height</th>
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<td>Dead</td>
<td>Percent</td>
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<td>Dead</td>
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<td>22.1</td>
<td>19.8</td>
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</table>

**Thinned**

**Unthinned**

Figure 2—Smoothed curves for a 23-day period contrasting phgeom and bark surface temperatures on the south side of two lodgepole pine trees between a thinned and unthinned stand.

Temperature (1 Day)—More details are shown when smoothing is done over a 24-hour period. Three typical curves (fig. 5) are shown for temperatures recorded on the north side of the sample trees at breast height. First, we see a reversal in dominance between surface and phgeom temperatures both in the thinned stand (fig. 5A) and the unthinned stand (fig. 5B). Variability magnitude varies from 0 and 7°C. After sunrise, there is a reversal in the temperature curves, with the phgeom temperature higher than the surface temperature. The surface heat buildup accelerates, and by afternoon surface temperature again becomes dominant and remains so until the following morning.

Taking this comparison further, we contrasted the phgeom temperature curves for the thinned and unthinned stands (fig. 5C). During late afternoon, there was a peak difference of 8°C, while during the remainder of the day the two smoothed curves are quite similar. The thinned stand had more heat building up in the phgeom than did the unthinned stand.

Solar (23 days)—Incident solar radiation is a measure of the amount of sunlight that strikes the tree surface or forest floor and was expected to be strongly correlated with temperature recorded for various points on or near the sample trees.

The hourly averages for incoming solar radiation were smoothed to show the daily solar curve for the 23 days. Marked differences in solar radiation were observed between the thinned and unthinned stand at breast height (fig. 5A), while no such striking difference was shown for the sensors placed on the trees (fig. 5B). It may be hard to interpret trends seen here, particularly those at breast height, because sensors placed on trees were influenced by occasional shade from various parts of the tree. Therefore, the tower sensors were included to serve as a reference for incoming solar radiation.

The spread in the values obtained on the trees at breast height was greater than the values obtained from the tower. Therefore, it is assumed that shading is not a part in the measurement of the factors in figure 5A.

Solar (5 Days)—The daily solar radiation curves smoothed over a 5-day period more explicitly showed the separation we observed earlier (fig. 6A and 6B). Less separation was observed in the two smoothed curves at breast height near the sampled trees when compared to the amount of sunlight striking the sensors on the instrument towers. These differences reflect, in part, placement of the sensors in the stands. Those sensors in the inter-space (on the towers) are probably more representative of measured incident solar radiation within the stands.

Wind speed (23 days)—Wind speed was not smoothed as much as the previously mentioned factors. It allowed some of the variance to remain in the data to more clearly show trends. During a 24-hour period, wind speed as measured on the tower varied between 1.6 and 5.6 km/h (fig. 7). The thinned stand had higher wind speed than the unthinned stand. The average (or overall) difference was only about 1.6 km/h. However, during the period of most MPR flight, between 4 and 6 p.m. (Glasman 1974), the difference was consistently 3.2 or more km/h.

Most wind movement occurred at the tower in the thinned stand, while the least movement was within the crown in the unthinned stand. Wind speed varied between 1.6 and 4.8 km/h (fig. 8).

Wind speed (5 Days)—Consistency resulted between the thinned and unthinned smoothed curves (fig. 9) for wind speed on the instrument tower. This set of curves was very uniform for the 5 days. However, smoothed averages for the difference between the two curves varied from 1.0 to 1.8 km/h.
<table>
<thead>
<tr>
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<th>Crown length/percentage of total height</th>
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**Figure 3**—Smoothed curves for a 5-day period contrasting phloem and bark surface temperatures on the south side of a lodgepole pine tree in a thinned stand.

**Figure 4**—Smoothed curves for a 5-day period contrasting bark surface temperatures on the south side of two lodgepole pine trees between a thinned and unthinned stand.

**Temperature (1 Day)**—More details are shown when smoothing is done over a 24-hour period. Three typical curves (fig. 4) are shown for temperatures recorded on the north side of the sample trees at breast height. First, we see a reversal in dominance between surface and phloem temperatures both in the thinned stand (fig. 5A) and the unthinned stand (fig. 5B). Magnitude varies between 0 and 7°C. After sunset, there is a reversal in the temperature curves, with the phloem temperature higher than the surface temperature. The surface heat build-up accelerates, and by afternoon surface temperature again becomes dominant and remains so until the following morning.

**Wind speed (32 days)**—Wind speed was not smoothed as much as the previously mentioned factors. This allowed some of the variance to remain in the data to more clearly show trends. During a 24-hour period, wind speed as measured on the tower varied between 1.6 and 5.6 km/h (fig. 6). The thinned stand had higher wind speed than the unthinned stand. The average (or overall) differences were only about 1.6 km/h. However, during the period of most MPB flight, between 4 and 6 p.m. (Basu-ness 1974), the difference was consistently 3.2 or more km/h.

The spread in the values obtained on the trees at breast height was greater than the values obtained from the tower. Therefore, it is assumed that shading is playing a part in the measurement of the factors in figure 6A.

**Solar (5 Days)**—The daily solar radiation curves smoothed over a 5-day period more explicitly showed the separation we observed earlier (fig. 6A and 6B). Less separation was observed in the two smoothed curves at breast height near the sampled trees when compared to the amount of sunlight striking the sensors on the instrument towers. These differences reflect, in part, placement of the sensors in the stands. Those sensors in the inter-sinus (on the towers) are probably more representative of measured incident solar radiation within the stands.

**Wind speed (32 days)**—Wind speed was not smoothed as much as the previously mentioned factors. This allowed some of the variance to remain in the data to more clearly show trends. During a 24-hour period, wind speed as measured on the tower varied between 1.6 and 5.6 km/h (fig. 7). The thinned stand had higher wind speed than the unthinned stand. The average (or overall) differences were only about 1.6 km/h. However, during the period of most MPB flight, between 4 and 6 p.m. (Basu-ness 1974), the difference was consistently 3.2 or more km/h.

Most wind movement occurred at the tower in the thinned stand, while the least movement was within the crown in the unthinned stand. Wind speed varied between 1.6 and 4.8 km/h (fig. 8).

**Wind speed (5 Days)**—Consistency resulted between the thinned and unthinned smoothed curves (fig. 9) for wind speed in the instrument tower. This set of curves was very uniform for the 5 days. However, smoothed averages for the difference between the two curves varied from 1.9 to 1.6 km/h.

**Figure 5**—An example of the daily solar radiation curve showing the daily solar radiation and its difference between thinned and unthinned stands.
Figure 5—Smoothed curves for a 24-hour period (August 3, 1989). Temperatures at breast height on the north side of the tree are contrasted between (A) bark surface and phloem-thinned; (B) bark surface and phloem-unthinned; and (C) thinned and unthinned phloem.

Figure 6—Smoothed curves for a 23-day period contrasting wind speed on the instrument tower between a thinned and unthinned lodgepole pine stand.

Figure 7—Smoothed curves for a 23-day period contrasting wind speed on the instrument tower and in the crown between a thinned and unthinned lodgepole pine stand.

Figure 8—Smoothed curves for a 23-day period contrasting wind speed on the instrument tower and in the crown between a thinned and unthinned lodgepole pine stand.

Figure 9—Smoothed curves for a 5-day period contrasting wind speed on the instrument tower between a thinned and unthinned lodgepole pine stand.

Figure 10—Smoothed curves for a 23-day period contrasting wind speed on the instrument tower between a thinned and unthinned lodgepole pine stand.

Figure 11—Smoothed curves for a 23-day period contrasting wind speed on the instrument tower and in the crown between a thinned and unthinned lodgepole pine stand.

Figure 12—Smoothed curves for a 23-day period contrasting wind speed on the instrument tower and in the crown between a thinned and unthinned lodgepole pine stand.

Beetle Response

The number of MPB caught in pheromone-baited traps in a thinned stand was only about 5 percent of the total caught in both thinned and unthinned stands. These stands were 1 km from stands where microclimate measures were made. The average numbers of beetles caught per trap were thinned Z = 8.7, unthinned Z = 159.1. Most trapped beetles were females, with a higher percentage being caught in thinned than unthinned stands (thinned = 88.5 percent female; unthinned = 81.2 percent female) (Table 3). Stands in which microclimate measures were made had 14.2 trees/ha (2.0 percent) killed by MPB in the thinned stands compared to 174.1 trees/ha (16.0 percent) killed in the unthinned stand.
Figure 7—Smoothed curves for a 23-day period contrasting wind speed on the instrument tower between a thinned and unthinned lodgepole pine stand.

Figure 8—Smoothed curves for a 23-day period contrasting wind speed on the instrument tower and in the crown between a thinned and unthinned lodgepole pine stand.

Figure 9—Smoothed curves for a 5-day period contrasting wind speed on the instrument tower between a thinned and unthinned lodgepole pine stand.

Figure 9—Smoothed curves for a 5-day period contrasting wind speed on the instrument tower between a thinned and unthinned lodgepole pine stand.

Figure 6—Smoothed curves for a 23-day period contrasting breast height (A) and lower (B) solar radiation between a thinned and unthinned lodgepole pine stand.

Figure 5—Smoothed curves for a 24-hour period (August 3, 1986). Temperatures at breast height on the north side of the tree are contrasted between (A) bark surface and phloem-thinned; (B) bark surface and phloem-untrenched; and (C) thinned and unthinned phloem.

Figure 4—Smoothed curves for a 23-day period contrasting wind speed on the instrument tower between a thinned and unthinned lodgepole pine stand.

Figure 3—Smoothed curves for a 23-day period contrasting wind speed on the instrument tower and in the crown between a thinned and unthinned lodgepole pine stand.

between 200° and 250° for the 23-day period. The larger range in wind direction for the 5 days shows that some detail is being lost when smoothing techniques are used over longer periods. As in the 23-day period, no major difference in wind direction occurred between the thinned and unthinned stands.

Stand Temperatures—Temperatures of the ground and north side of trees were significantly higher (P < 0.05) in thinned than unthinned stands (ground temperature: thinned $x = 30.8^\circ$C; unthinned $x = 26.0^\circ$C) and south side at breast height (thinned $x = 26.6^\circ$C; unthinned $x = 24.3^\circ$C). North sides of trees were not significantly different (thinned $x = 24.2^\circ$C; unthinned $x = 22.9^\circ$C) (Table 5).

Beetle Response

The number of MBP caught in pheromone-baited traps in a thinned stand was only about 5 percent of the total caught in both thinned and unthinned stands. These stands were 1 km from stands where microtome measures were made. The average numbers of beetles caught per trap were: thinned $x = 8.7$; unthinned $x = 129.2$. Most trapped beetles were females, with a higher percentage being caught in thinned than unthinned stands (thinned 68.5 percent female; unthinned 81.2 percent female) (Table 6). Stands in which microtome measures were made had 14.2 trees/ha (2.0 percent) killed by MBP in the thinned stands compared to 17.4 trees/ha (16.0 percent) killed in the unthinned stand.
The higher temperatures on south sides of trees in thinned stands could be a deterrent to MBP feeding and boring into the bark. In our study, south-side temperatures between 10 a.m. and 2 p.m. averaged 2.5°C higher than those on north sides, and the maximum temperature 19°C higher in the thinned stand. Powell (1967) reported subcortical temperatures were occasionally 35°C higher than those outside. Beetles emerge at a greater rate from south than north sides of trees (Safariky and Jahren 1970). North-side temperatures in thinnings in our study would have been a deterrent to beetle infestation and offer more favorable physical environment than south-side temperatures for attacking MBP. Beetle attack density may be dependent on the degree of thinning on north sides (Reid 1965; Shepard 1985), and when trees are strip-stripped, the attacks usually occur on norther and east sides (Mitchell and others 1983).

The effect of temperature could be more subtle than a direct inceptible physical environment on south sides of trees. Mountain pine beetles may have evolved behavior to avoid situations where their brood are not likely to survive. In thinned stands, where tree temperatures are a few degrees above those of trees in unthinned stands, MBP may proceed too far in their development before winter, thus entering winter in stages that are susceptible to freezing—for example, the pupal stages as observed by Reid (1965) and Amman (1975).

Another way that MBP behavior may be affected by thinning is through the disruption of pheromone communication system. More sunlight penetrates the canopy in the thinned than unthinned stands, resulting in significantly higher soil temperatures. The increased soil temperatures, which averaged 4.8°C higher in the thinned than in the unthinned stand in this study, increase convection currents (Rosberg and others 1983) and air turbulence that could disrupt pheromone plumes and resultant MBP communication. In addition, wind speed is greater in thinned than unthinned stands, thus possibly further complicating pheromone communications by MBP. Beetle response to pheromones is more predictable at windspeeds under 5 km/h, but a few beetles flew at 7.5 km/h (Gray and others 1972). Twice as many males as females flew at wind speeds in excess of 4 km/h.

In dense stands sunlight is absorbed by the upper levels of the tree canopy that in turn hinders the surrounding air, creating instability in the air within the upper canopy. This creates an inversion in the stem zone that is characterized by more stable air (Chapman 1967; Fares and others 1980). Inversion layers tend to be more pronounced in dense stands than in sparse ones (Fares and others 1980; Fritschler 1984). Aeromicro movement below a dense canopy on a sunny day is trapped beneath the canopy until it flows to a point where the canopy is less dense or has an opening (Fares and others 1980). Solar energy penetrating through canopy openings to the forest floor heats the ground and adjacent air, which becomes buoyant and rises through the canopy opening, carrying the aeromicro with it (Fares and others 1980). The aeromicro or pheromone plume would be torn apart in the follower, more turbulent air currents above the canopy. Therefore, when MBP infest a tree in a recently thinned stand, canopy density usually is insufficient to trap the pheromone and move it horizontally to attract other beetles. Rather, the pheromone rises through the canopy convection currents and is dispersed above the canopy. Smith and others (in press) concluded that most MBP fly in the hole area beneath the canopy where the pheromone communication system would be most effective.

When MBP do infest a tree in a thinned stand of lodgepole pine, usually only the single tree is infested, and occasionally a nearby tree when spacing is not maintained. The openness of the stand causes convection currents over the stand so that the pheromone plume around infested trees vertically out of the stand rather than horizontally. Thus, the infestation of other stands is dependent on the degree of thinning. Older thinnings will probably provide a suitable environment for MBP. As the thinned stand matures, shade will increase and light and temperature decrease because of increased crown size, development of a shrub and young tree layer, and failure of limbs to prune. Therefore, stand microclimate will likely become conducive to beetle infestation before tree competition becomes severe.

**DISCUSSION**

Our discussion centers on the three areas outlined in the Results section.

**Stand Characteristics**

The principal difference between the thinned and unthinned stands used in this microclimatic study was the two measures of density. Basal area was 14.9 m²/ha and numbers of trees 882.25 ha less in the thinned than unthinned stand. The average diameters of trees in both thinned and unthinned stands did not differ significantly. The difference in density appears to be responsible for the differences in microclimate between the two stands.

**Stand Microclimate**

Microclimatic observations showed consistent differences between the thinned and unthinned stands. Thinning lodgepole pine stands results in increased light intensity, wind movement, insolation, and temperature. These factors, either separately or in various combinations, appear to affect MBP activity. The differences observed between thinned and unthinned stands are sometimes quite subtle. However, even minor changes in microclimate could have profound effects on MBP.
Table 2—Tree and soil temperatures (°C) in thinned and unthinned lodgepole pine stands obtained by infrared thermometer, August 13, 1966, in northern Utah.

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<tr>
<td>Tree south side</td>
<td>17</td>
<td>33</td>
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</tbody>
</table>

Number of observations in each stand. Mean in rows followed by different letters are significantly different (P<.05).

Table 3—Numbers of mountain pine beetle caught August 21 to September 5, 1966, in Lindgren traps baited with mountain pine beetle lure and placed in thinned and unthinned lodgepole pine stands in northern Utah.

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DISCUSSION

Our discussion centers on the three areas outlined in the Forest section.

Stand Characteristics

The principal difference between the thinned and unthinned stands used in this microclimatic study was the two measures of density. Basel area was 14.9 m²/ha and numbers were 126.2/ha in the thinned stand and 19.8/ha in the unthinned stand. The average diameters of trees in both thinned and unthinned stands did not differ significantly. The data suggests that the difference in microclimate might be responsible for the differences in microclimate in the two stands.

Stand Microclimate

Microclimatic observations showed consistent differences between the thinned and unthinned stands. Thinning lodgepole pine stands results in increased light intensity, wind movement, insolation, and temperature factors, either separately or in various combinations, appear to affect MIP activity. The differences observed between thinned and unthinned stands are sometimes quite subtle. However, even minor changes in microclimate could have profound effects on MIP.

The higher temperatures on south sides of trees in thinned stands could be a deterrent to MIP landing and biting into the bark. In our study, south-side temperatures between 10 a.m. and 2 p.m. averaged 2.3°C higher than those on north sides, with the maximum temperature 12°C higher in the thinned than unthinned stand. Powell (1967) reported subthermal temperatures were occasionally 35°C higher on south sides than north sides. Beele emerges at a greater rate from south than north sides of trees (Hoffert and Hurley 1970). South-side temperatures in thinning of this study would not have been a deterrent to beetle infestation and offer more favorable environmental conditions for attack MIP. Beele attack densities are higher on north sides (Reid 1966; Schmitt 1965), and when these trees are strip-stocked, the attacks commonly occur on north and east sides (Mitchell and others 1983).

The effect of temperature could be more subtle than a direct, hopeless physical environmental factor on south sides of trees. Mountain pine beetles may have evolved behavior to avoid situations where their brood are not likely to survive. In thinned stands, where tree temperatures are a few degrees above those of trees in unthinned stands, MIP may proceed too far in their development before winter, thus entering winter in stages that are susceptible to freezing—e.g., the pupal stage as observed by Reid (1968) and Arman (1973).

Another way that MIP behavior may be affected by thinning is through the disruption of the pheromone communication system. More sunlight penetrates the canopy in the thinned than unthinned stands, resulting in significantly higher soil temperatures. The increased soil temperatures, which averaged 3.8°C higher in the thinned than in the unthinned stand in this study, increase convection currents (Rosenberg and others 1983) and air turbulence that could disrupt pheromone plumes and result in MIP communication. In addition, wind speeds are greater in the thinned than unthinned stands, thus possibly further complicating pheromone communications by MIP. Beele response to pheromone is more predictable at wind speeds under 5 km/h, but a few beetles flew at 7.5 km/h (Gray and others 1972). Twice as many males as females flew at windspeeds in excess of 4 km/h.

In dense stands sunlight is absorbed by the upper levels of the tree canopy that in turn heats the surrounding air, creating instability in the air within the upper canopy. This creates an inversion in the stem zone that is characterized by more stable air (Clagman 1967; Fares and others 1980). Inversion tends to be more pronounced in denser stands than in sparse ones (Fares and others 1980; Pritsch 1984). Aerosol movement below a dense canopy on a sunny day is trapped beneath the canopy until it flows to a point where the canopy is less dense or has an opening (Fares and others 1980). Solar energy penetrating through canopy openings to the forest floor heats the ground and adjacent air, which becomes buoyant and rises through the canopy opening, carrying the aerosol with it (Fares and others 1980). The aerosol or pheromone plume would be torn apart in the faster, more turbulent air currents above the canopy. Therefore, when MIP infest a tree in a recently thinned stand, canopy density usually is insufficient to trap the pheromone and move it horizontally to attract other beetles. Rather, the pheromone plumes through the canopy on convection currents and are dispersed above the canopy. Schmitt and others (in press) concluded that most MIP fly in the hole area beneath the canopy where the pheromone communication system would be most effective. When MIP do infest a tree in a thinned stand of lodgepole pine, a single tree is infested, and occasionally a nearby tree when spacing is not maintained. The openness of the stand causes convection current created by solar insolation to transport the pheromone plume around infested trees vertically out of the stand rather than horizontally. Thus, the infestation of other trees would be dependent on the degree of the pheromone plume around infested trees vertically out of the stand rather than horizontally. Older thinnings will probably provide a suitable environment for MIP. As the thinned stand matures, shade will increase and temperature decrease because of increased crown size, development of a shrub and young tree layer, and failure of limbs to prune. Therefore, stand microclimate will likely become conducive to beetle infestation before tree competition becomes severe.

Beele Response

Mountain pine beetle response to baited funnel traps was much less in an unthinned stand than in an unthinned stand located 1 km from stands that contained weather instruments, with only about 6 percent of total beetle infestations in the thinned stand. Beetles may have passed through the thinned stand without detecting a point source of aggregative pheromone. Beetle abundance was also reflected by the percentage of trees killed, which was much less (2 percent) in the thinned stand than in the unthinned stand (16 percent) where weather instruments were located. Schmitt and others (in press) caught fewer beetles in passive traps in heavily thinned than in lightly thinned and check stands in Montrose, and McGregor and others (1987) found significantly fewer insects in trees in heavily thinned and check stands. Because air temperatures in thinned and unthinned stands are about the same, beetles may sense the difference in light intensity or the greater air turbulence in thinned stands and avoid the open stand. Light could serve as an integrator of other microclimatic features such as temperature, humidity, and air turbulence. Schmitt (1966) showed in laboratory studies that MIP increased attempts to fly as light intensity and temperature increased.

Our observations suggest microclimate could play a significant role in MIP behavior in lodgepole pine stands. Infestation rates of LPP stands could possibly be assessed by monitoring stand microclimate, specifically light. If microclimate changes are responsible for keeping beetles out of an LPP stand, they could be assessed by watching weather instruments and then by watching the microclimate directly. If microclimate changes are responsible for keeping beetles out of thinned stands, financial managers could use information from stand microclimate to minimize beetle infestation. At the moment, it is not possible to cut or thin stands, a favorable microclimate may occur and invite beetle attack, regardless of tree vigor. Additional studies are needed to determine the effect of thinning and unthinned stands to determine more definitively microclimatic thresholds of MIP infestation and the association of thresholds with tree vigor levels.
REFERENCES


Thinning lodgepole pine stands increased light intensity, wind movement, insolation, and temperature. Temperatures on the south exposure of tree trunks and of soil were significantly higher in thinned than unthinned stands. Light and wind also were higher in the thinned stand. Fewer mountain pine beetles were caught in pheromone-baited traps in a thinned than in an adjacent unthinned stand. Percentage of trees killed by mountain pine beetles was only 2 percent in a thinned stand compared to 16 percent in an adjacent unthinned stand.

KEYWORDS: Pinus contorta, Dendroctonus ponderosae, pheromone, lodgepole pine
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